

Complete larval development of the hermit crabs *Clibanarius aequabilis* and *Clibanarius erythropus* (Decapoda: Anomura: Diogenidae), under laboratory conditions, with a revision of the larval features of genus *Clibanarius*

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Abstract The complete larval development (four zoeae and one megalopa) of *Clibanarius aequabilis* and *C. erythropus*, reared under laboratory conditions, is described and illustrated. The larval stages of the two northeastern Atlantic *Clibanarius* species cannot be easily differentiated. Their morphological characters are compared with those of other known *Clibanarius* larvae. The genus *Clibanarius* is very homogeneous with respect to larval characters. All *Clibanarius* zoeae display a broad and blunt rostrum, smooth abdominal segments and an antennal scale without a terminal spine. Beyond the second zoeal stage, the fourth telson process is present as a fused spine, and the uropods are biramous. In the fourth larval stage all species display a mandibular palp. The *Clibanarius* megalopa presents weakly developed or no ocular scales, symmetrical chelipeds, apically curved corneous dactylus in the second and third pereopods, and 5–11 setae on the posterior margin of the telson. Apart from the number of zoeal stages, *Clibanarius* species may be separated, beyond the second zoeal stage, by the telson formula and the morphology of the fourth telson process.

Keywords *Clibanarius aequabilis* · *Clibanarius erythropus* · Decapoda · Diogenidae · Larval development

Introduction

The larval development of *Clibanarius* species has deserved special attention and has been described for over 13 species. Brossi-Garcia (1987) compiled the larval morphological characters of most *Clibanarius* species described, and highlighted the conservative developmental pattern of the genus. Siddiqui et al. (1991, 1993) confirmed the existence of this developmental pattern among *Clibanarius* species, but also noticed the occurrence of small intraspecific variations.

The hermit crabs *Clibanarius aequabilis* Dana, 1851 and *Clibanarius erythropus* (Latreille, 1818) are both present in the eastern Atlantic. The first occurs around Madeira and the Canary and Cape Verde islands; the second occurs on European Atlantic shores, in the Mediterranean Sea and at the Azores (Udekem d'Acoz 1999; González-Gordillo et al. 2001). In the present paper we describe the complete larval series of *C. aequabilis* and compare it with previously described larval stages of other species of the genus, particularly with those of *C. erythropus*. Despite the fact that these two eastern Atlantic species do not co-occur in the same area, a careful comparison seemed to be required. In this way, the larval morphology of *C. erythropus* was redescribed following modern standards. The general features of *Clibanarius* larvae are revised and discussed.

Methods

Five ovigerous *Clibanarius aequabilis* females were hand-collected during March 2003 in the intertidal region at Reis Magos (32°38.4' N, 16°50.7' W), Madeira Island, Portugal, and transported to the laboratory. Until hatching of their

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larvae, females were kept in darkness, in a 180 l tank connected to a larval collector, at a salinity of 34 ± 1 and a temperature of $24 \pm 1^\circ \text{C}$. The most active larvae (those displaying pronounced positive phototactic responses) from five different ovigerous hermit crabs were randomly selected and stocked at a density of 20 larvae l^{-1} in four 10 l small research scale-rearing tanks described by Calado et al. (2003). Seawater was UV-sterilized and $1 \mu\text{m}$ -filtered, had a salinity of 34 ± 1 , and the temperature was kept stable at $24 \pm 1^\circ \text{C}$ through a heating/cooling system. The tanks were illuminated from above with fluorescent light, with a photoperiod of LD 14:10. Ammonia and nitrite were monitored daily and maintained below detectable levels. Nitrate and pH showed average values (\pm standard deviation) of $4 (\pm 1)$ and $8.1 (\pm 0.1) \text{ mg l}^{-1}$, respectively. *Artemia* cysts (Unibest[®] 020730) were hatched according to the procedures described by Sorgeloos et al. (1986). All larval stages were provided with live *Artemia* nauplii as prey at a density of 5,000 items l^{-1} . Ten haphazardly selected larvae were sampled daily and staged to determine stage duration. The sampled larvae were fixed in 4% formaldehyde.

For an adequate comparison, *C. erythropus* larvae were also cultured. Five ovigerous females were hand-collected during July 2005 in Ria do Alvor ($37^\circ 08' \text{N}$; $08^\circ 37' \text{W}$), Algarve, Portugal, and transported to the laboratory. *Clibanarius erythropus* larval culture followed the same methods as described for *C. aequabilis*.

Drawings and measurements were made with the aid of a camera lucida on a binocular Wild M8. Setal observations and drawings were made using a Zeiss microscope with camera lucida. Slides with appendages were prepared with Faure's liquid (Reyne 1949). Larval description followed the method proposed by Clark et al. (1998), and setal terminology is according to Ingle (1993) and Garm (2004). The long plumose setae on distal exopod segments were drawn truncated. Setal counts refer from proximal to distal sequence. The measurements taken were: the distance between the tip of the rostrum and the posterior end of the telson (TL), the carapace length from the tip of the rostrum to the posterior margin of the carapace (CL), and the rostrum length from the tip of the rostrum to the eye socket (R).

The spent females and complete larval series have been deposited in the Instituto Nacional de Investigação Agrária e Pescas (IPIMAR) in Lisbon, Portugal (numbers IPIMAR/D/Ca/12/2003 and IPIMAR/D/Ce/09/2005).

Results

Under laboratory conditions, *C. aequabilis* hatches as zoea and then passes through four zoeal stages and one

megalopa. The latter is reached after 8 days. The first and final larval stages are described in detail, while for the other larval stages only deviating characters are described.

Under laboratorial conditions, *Clibanarius erythropus* has a larval development similar to that of *C. aequabilis*. A detailed description of the first zoeal stage, following modern standards, is presented.

Clibanarius aequabilis Dana, 1851 (Figs. 1–5)

First zoea (Fig. 1a–j')

Dimension: TL = 2.39–2.62 mm; CL = 1.04–1.12 mm; R = 0.46–0.54 mm

Carapace (Fig. 1a, a'): without processes or spines, with the postero-lateral border smoothly rounded; rostrum broad, rather blunt with triangular pointed tip extending beyond antennal scale, rostrum about 0.89 ± 0.06 times the carapace; eyes compound and sessile.

Antennule (Fig. 1b): peduncle unsegmented, with 1 long plumose seta sub-terminally, 3 aesthetascs and 3 unequal simple setae terminally.

Antenna (Fig. 1c): protopod unsegmented with 1 small strong cuspidate seta; endopod extending beyond more than half the scaphocerite, with 3 long plumose setae on the posterior end; scaphocerite unsegmented, with 11 plumose setae.

Mandible (Fig. 1d): asymmetrical; palp absent.

Maxillule (Fig. 1e): coxal endite with 3 serrulate, 2 pappose and 2 simple setae; basal endite with 2 cuspidate and 2–3 simple setae; endopod with 1 + 1 + 2 simple setae.

Maxilla (Fig. 1f): coxal endite bilobed with 7 + 4 serrulate and papposerrate setae, basal endite bilobed with 5 + 4 papposerrate and simple setae; endopod unsegmented with 3 + 2 long simple setae and microtricha on outer margin; scaphognathite with 5 marginal plumose setae.

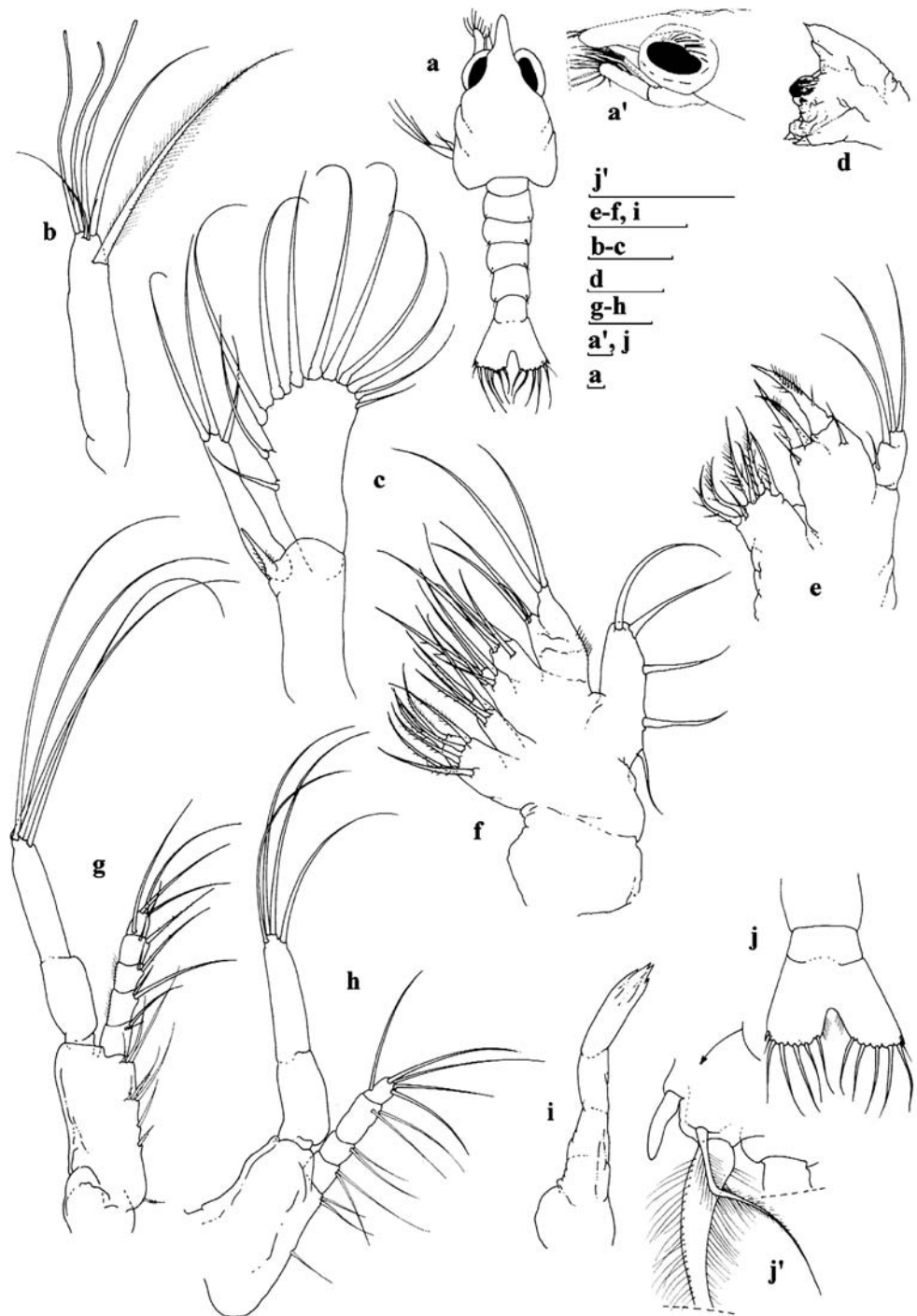
First maxilliped (Fig. 1g): coxa unarmed; basis with 1 + 1 + 1 + 3 + 3 papposerrate setae; endopod 5-segmented with 2, 2, 2, 2 and 1 + 4 papposerrate setae, microtricha on outer margin of second and third segments; exopod unsegmented, bearing 4 long plumose setae terminally.

Second maxilliped (Fig. 1h): coxa unarmed; basis with 1 + 2 papposerrate setae; endopod four-segmented with 2, 2, 2 and 1 + 4 papposerrate setae terminally. Exopod unsegmented, bearing 4 long plumose setae terminally.

Third maxilliped (Fig. 1i): long uniramous bud.

Pereiopods: absent.

Fig. 1 *Clibanarius aequabilis*. First zoea: **a** total animal, dorsal view; **a'** detail of rostrum, lateral view; **b** antennule; **c** antenna; **d** mandible; **e** maxillule; **f** maxilla; **g** first maxilliped; **h** second maxilliped; **i** third maxilliped; **j** telson; **j'** detail of posterior margin of telson. Scale bars 0.1 mm



Abdomen (Fig. 1a): five somites with margins rounded; with a pair of dorso-lateral marginal minute setae on somites 2–5; sixth somite feebly segmented.

Pleopods and uropods: absent.

Telson (Fig. 1a, j, j'): triangular, broader posteriorly with deep median cleft; with 7 + 7 processes; first process is a very short blunt spine, second process an anomuran hair, third to seven processes plumose setae, with the fourth being the longest.

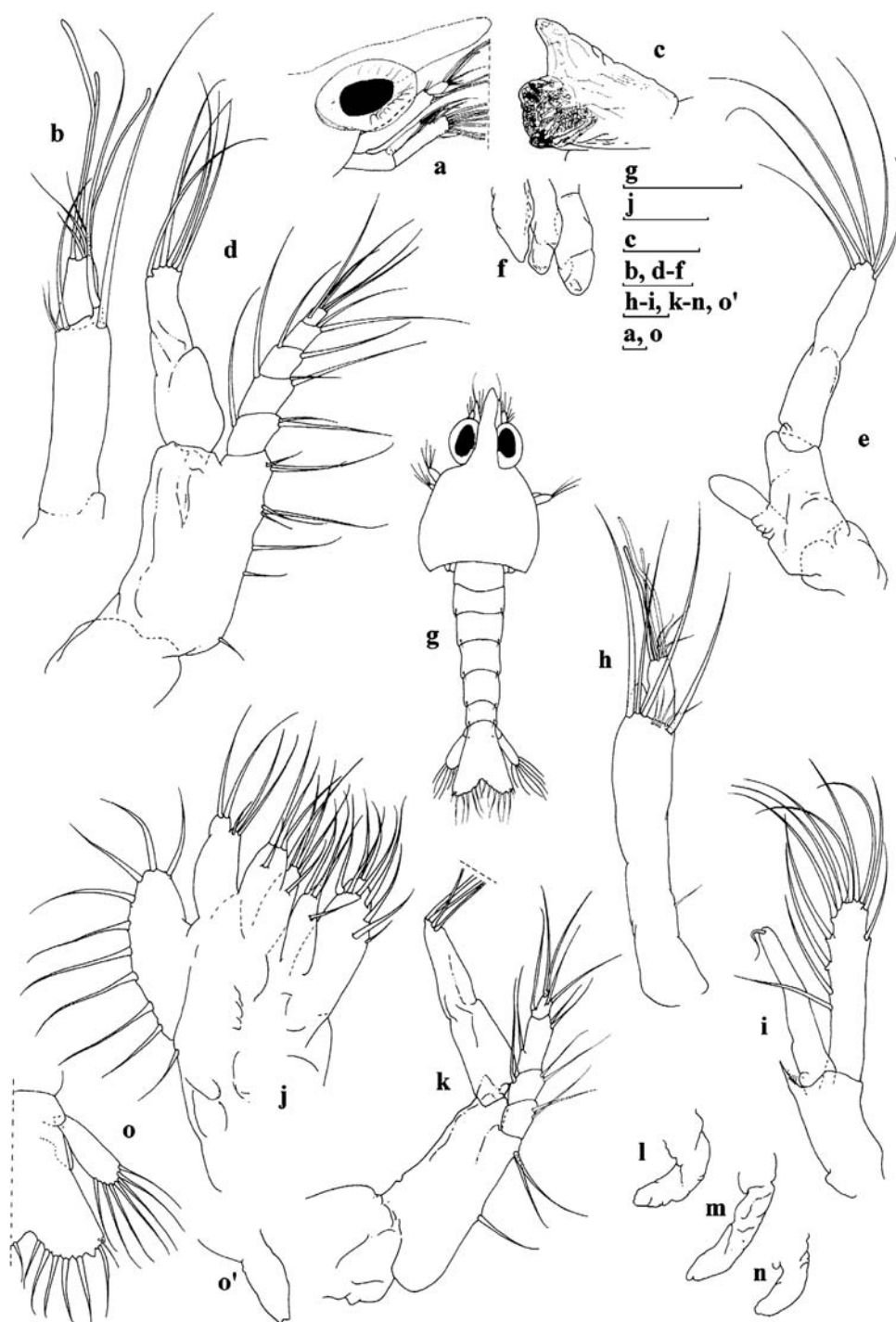
Second zoea (Fig. 2a–f)

Dimension: TL = 3.00–3.23 mm; CL = 1.31–1.39 mm; R = 0.58–0.65 mm

Carapace (Fig. 2a): eyes stalked; otherwise unchanged.

Antennule (Fig. 2a, b): peduncle unsegmented with 2 long plumose and 2 short simple setae terminally, 1 long plumose seta at site of future endopod; exopod bud clearly delineated, with 3 simple setae and 3 aesthetascs.

Fig. 2 *Clibanarius aequabilis*. Second zoea: **a** detail of rostrum, lateral view; **b** antennule; **c** mandible; **d** first maxilliped; **e** third maxilliped; **f** first to third pereopod. Third zoea: **g** total animal, dorsal view; **h** antennule; **i** antenna; **j** maxilla; **k** second maxilliped; **l** third pereopod; **m** fourth pereopod; **n** fifth pereopod; **o** telson and uropods; **o'** detail of endopod of uropods. Scale bars 1.0 mm (**g**); 0.1 mm (**b–f, h–o'**)



Antenna (Fig. 2a): unchanged except for size.

Mandible (Fig. 2c): molar process with several small denticles and without teeth; otherwise unchanged.

Maxillule: basal endite with 4 cuspidate and 2 simple setae; otherwise unchanged except for size.

Maxilla: scaphognathite with 7 marginal plumose setae; otherwise unchanged except for size.

First maxilliped (Fig. 2d): endopod five-segmented with 1 + 2, 1 + 2, 1 + 1, 2 papposerrate and 1 + 4 papposerrate

setae; exopod bearing six long plumose setae terminally; otherwise unchanged.

Second maxilliped: endopod four-segmented with 2, 1 + 2, 1 + 2 papposerrate and 1 + 4 papposerrate setae terminally. Exopod bearing 6 long plumose setae terminally; otherwise unchanged.

Third maxilliped (Fig. 2e): biramous; endopod represented by a small bud; exopod unsegmented, bearing 6 plumose setae.

First to third pereopods (Fig. 2f): present as small uniramous buds.

Abdomen: unchanged except for size.

Pleopods and uropods: absent.

Telson: 8 + 8 processes, with an additional inner pair of telson plumose setae; otherwise unchanged.

Third zoea (Fig. 2g–o')

Dimension: TL = 3.44–3.77 mm; CL = 1.61–1.72 mm; R = 0.75–0.81 mm

Carapace (Fig. 2g): unchanged except for size.

Antennule (Fig. 2h): peduncle unsegmented with 1 basal simple seta, 4 long plumose setae and 4 short simple setae terminally; inner flagellum small, bud-like; outer flagellum with 3 aesthetascs, 1 long plumose seta and 3 shorter simple setae.

Antenna (Fig. 2i): endopod as long as the scale, with 1 short simple seta in apical region; scaphocerite with 12 plumose setae. Otherwise unchanged.

Mandible and maxillule: unchanged except for size.

Maxilla (Fig. 2j): coxal endite with 9 + 4 serrulate and papposerrate setae; scaphognathite with 10–11 marginal plumose setae; otherwise unchanged except for size.

First, second (Fig. 2k) and third maxillipeds: unchanged except for size.

First pereopod: uniramous bud showing its chelate nature.

Second and third (Fig. 2l) pereopods: unchanged.

Fourth (Fig. 2m) and fifth (Fig. 2n) pereopods: uniramous buds.

Abdomen (Fig. 2g): abdominal somite 6 fully separated from telson, bearing a pair of minute dorso-lateral setae; otherwise unchanged.

Pleopods: absent.

Uropods (Figs. 2o, o'): biramous; exopods well developed, not reaching the end of telson, with 7–8 plumose setae; endopod small bud with 2 minute projections at its tip.

Telson (Fig. 2o): triangular, broader posteriorly with median cleft less pronounced; number of telson processes: 9–10 + 9–10 (first process as a very short blunt spine, second as an anomuran hair, third as a plumose seta, fourth as a very reduced fused spine and fifth to ninth or tenth processes as plumose setae). One individual in seven observed with 9 + 9 processes (additional inner pair of plumose telson setae, without reduced fused spine).

Fourth zoea (Fig. 3a–r)

Dimension: TL = 4.08–4.40 mm; CL = 1.92–2.08 mm; R = 0.88–0.96 mm

Carapace (Fig. 3a): unchanged except for size.

Antennule (Fig. 3b): peduncle unsegmented with 2 + 1 simple setae along lateral margin, 4 short simple and 4 long plumose setae distally; inner flagellum unsegmented, enlarged in size; outer flagellum with 2 + 2 + 2 + 1 aesthetascs, 2 long and 2 short plumose setae.

Antenna (Fig. 3c): endopod longer than antennal scale, two-segmented: first segment unarmed, second segment with a short simple seta and a pointed tip; scaphocerite with 12–13 plumose setae. Otherwise unchanged.

Mandible (Fig. 3d): differs from the previous stage by the presence of an unsegmented palp.

Maxillule (Fig. 3e): coxal endite with 3 papposerrate, 2 pappose and 3 simple setae; otherwise unchanged.

Maxilla (Fig. 3f): coxal endite with 11–12 + 4 serrulate and papposerrate setae; basal endite with 7 + 6 papposerrate and simple setae; endopod unsegmented, bilobed, terminally bearing 3 + 2 long simple setae; scaphognathite with 15–17 marginal plumose setae, inferior lobe without setae.

First (Fig. 3g) and second maxillipeds: unchanged.

Third maxilliped (Fig. 3h): endopod two-segmented, incomplete 2–5 segments with two-minute projections at its tip; otherwise unchanged.

First pereopod (Fig. 3i): cheliped with chela enlarged, dactyl distinct, coxa, and merus clearly delineated, with tubercles on surface.

Second and third pereopods (Fig. 3j, k): long, the first six segments clearly delineated, coxa and merus with some tubercles on surface.

Fourth and fifth pereopods (Fig. 3l, m): short, with some segments clearly delineated.

Abdomen (Fig. 3a): unchanged except for size.

Pleopods (Fig. 3n–q): present as biramous buds on segments 2–5.

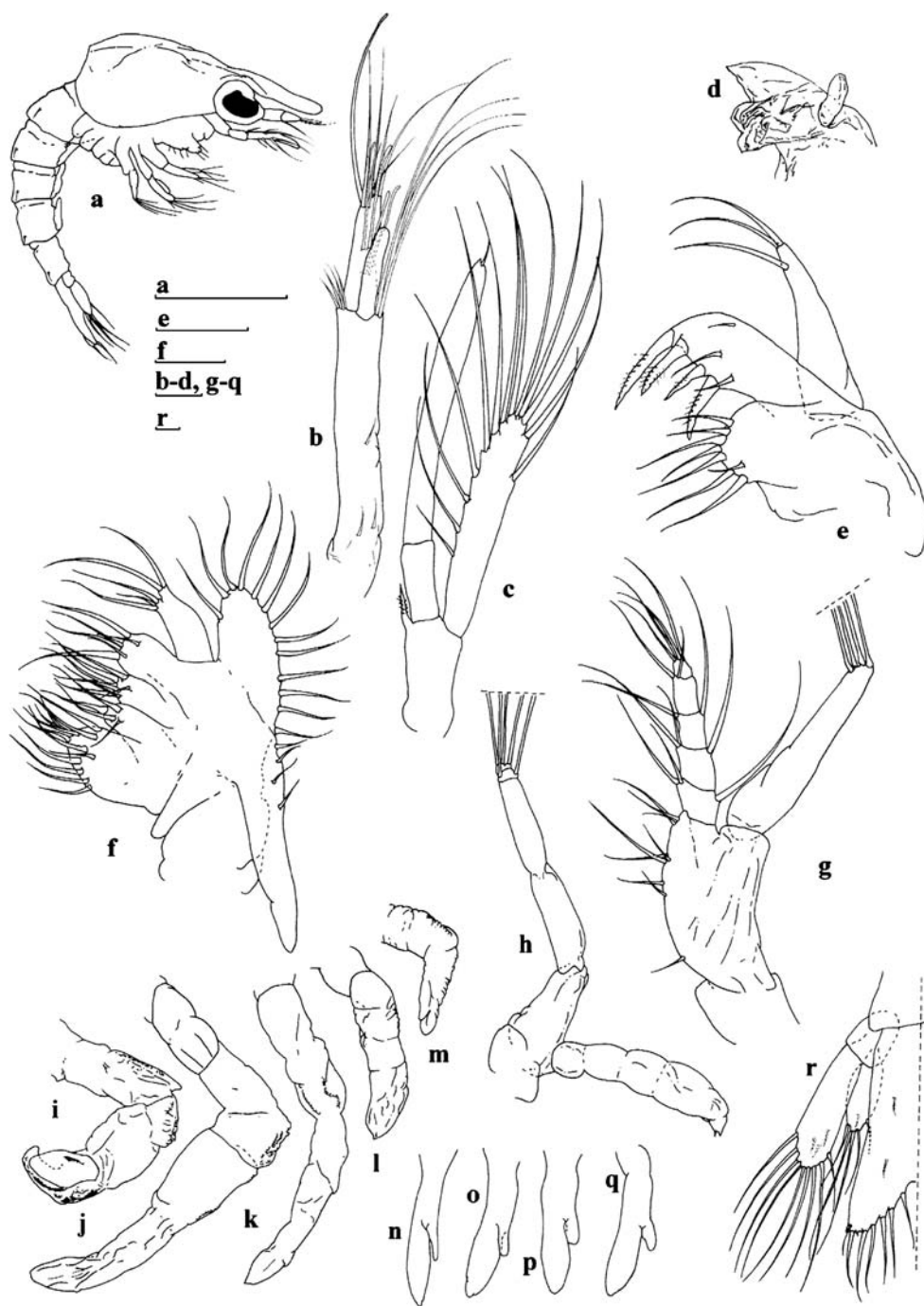
Uropods (Fig. 3r): total individualization of protopod, exopod and endopod; exopod with 8–9 plumose setae on apical region and 3–4 papposerrate setae on ventral surface; endopod smaller with 5 plumose setae on apical region and 1 pappose seta on ventral surface.

Telson (Fig. 3r): almost rectangular in shape; number of telson processes: 9 + 9–10 (first process as a very short blunt spine, second as an anomuran hair, third as a plumose seta, fourth as a very reduced fused spine and fifth to ninth or tenth processes as plumose setae); presence of two pairs of pappose setae on dorsal surface.

Megalopa (Figs. 4, 5)

Dimension: TL = 2.85–3.04 mm; CL = 1.08–1.15 mm; R = 0.15–0.19 mm

Fig. 3 *Clibanarius aequabilis*. Fourth zoea: **a** total animal, lateral view; **b** antennule; **c** antenna; **d** mandible; **e** maxillule; **f** maxilla; **g** first maxilliped; **h** third maxilliped; **i** first pereopod; **j** second pereopod; **k** third pereopod; **l** fourth pereopod; **m** fifth pereopod; **n–q** pleopods of abdominal somites 2–5; **r** telson and uropods. Scale bars 1.0 mm (**a**); 0.1 mm (**b–r**)



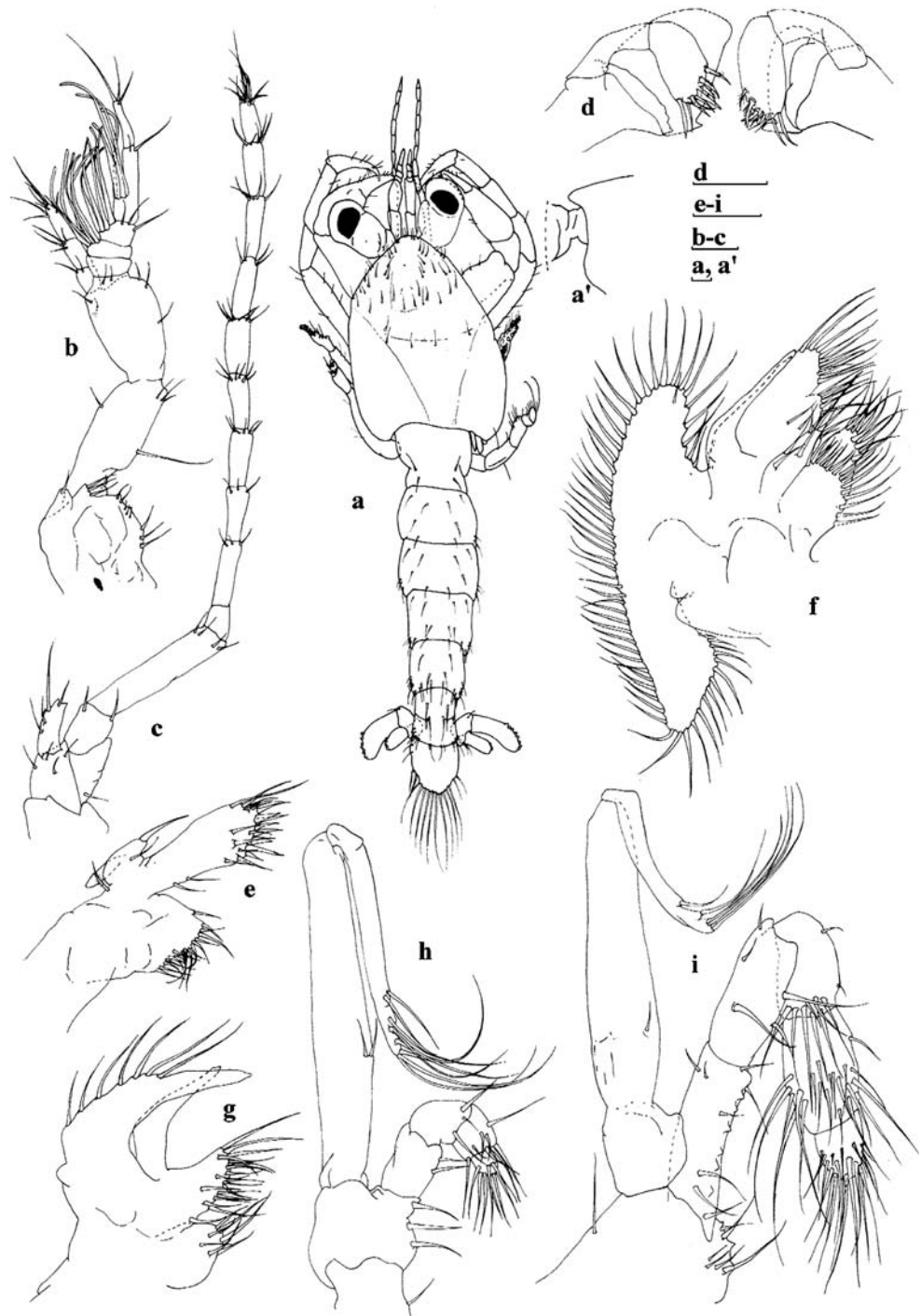
Carapace (Fig. 4a, a'): smooth, slightly broader than long; rostrum broad and blunt; ocular peduncles stout reaching the end of the antennular peduncle; ocular acicles not developed; surface and margins with proboscate setae distributed as figured.

Antennule (Fig. 4b): peduncle three-segmented, proximal segment with 12–13 papposerrate and simple setae; second segment with 1 long and 3–4 short simple setae and 1 papposerrate seta; distal segment with 6 simple setae; outer flagellum five-segmented, proximal segment

unarmed, second segment with 5 aesthetascs, third segment with 5 aesthetascs and 3 simple setae, fourth segment with fourth aesthetascs and 2–3 simple setae terminally, distal segment with three simple setae; inner flagellum three-segmented with two, four, and seven simple setae.

Antenna (Fig. 4c): basis with 3–4 simple setae, peduncle three-segmented with 1, 2, 3–4 simple setae; flagellum composed of 10 segments, each with 0–6 simple setae on distal margin, arranged as figured, except for the distal segment which has 9 simple setae on distal margin; acicle

Fig. 4 *Clibanarius aequabilis*. Megalopa: **a** total animal, dorsal view; **a'** detail of rostrum, lateral view; **b** antennule; **c** antenna; **d** mandibles; **e** maxillule; **f** maxilla; **g** first maxilliped; **h** second maxilliped; **i** third maxilliped. Scale bars 0.1 mm



with 1 spine-like projection on lateral margin, 4 simple setae and bifid spinous tip.

Mandibles (Fig. 4d): reduced and simplified, lower extremities of the incisor part with processes as illustrated; palp two-segmented, with 4–5 simple setae and 4 serrulate setae on the distal segment.

Maxillule (Fig. 4e): coxa with 18–21 papposerrate and simple setae; basis with 2 simple setae on the lateral inner margin and 5 cuspidate, 4 serrulate, 5–7 papposerrate, 3–4

simple and 1 long plumose setae on the distal margin; endopod unsegmented with 1 + 1 simple setae; 1 plumose seta present on the inner margin of basis.

Maxilla (Fig. 4f): coxa bilobed with 25–32 + 7–9 papposerrate and simple setae; basis bilobed with 8–10 + 11–13 papposerrate and simple setae; endopod unsegmented without seta; scaphognathite with 50–58 plumose setae on the distal margin and 1 simple seta on the dorsal surface of the upper lobe.

First maxilliped (Fig. 4g): coxa with 3–4 simple, 3 pappose and 1 papposerrate setae; basis with 4 simple, 3 serrulate and 11–14 papposerrate setae; endopod unsegmented without seta; exopod unsegmented with 7–9 plumose setae on the outer margin.

Second maxilliped (Fig. 4h): coxa with 1 simple seta; basis with 3 pappose setae; endopod four-segmented, proximal segment with 1 + 1 simple seta, second segment with 3 simple setae, third segment with 8 simple and papposerrate setae, and 7–8 papposerrate setae on the distal segment; exopod two-segmented, proximal segment with 2 simple setae and the distal segment with 6–8 plumose setae terminally.

Third maxilliped (Fig. 4i): basis with 6–7 simple setae and 3–4 sub-acute processes; endopod five-segmented, ischium with 8–10 simple seta and 5–6 sub-acute processes on *crista dentata*, merus with 4–6 simple setae, carpus with 9–10 simple setae, propodus with 5 simple, 2 cuspidate, and 13–14 papposerrate setae, and dactyl with 4 serrate, 7–8 simple, 2 cuspidate and 6 papposerrate setae; exopod 2-segmented with 1 simple seta on proximal segment and 6–8 (2 + 4 or 2 + 2 + 4) plumose setae terminally on distal segment.

First pereopod (Fig. 5a, a'): chelae equal, coxa with 6–8 simple setae; basis with 4–5 simple setae; ischium with 6–7 simple setae; merus, longest segment, with 14–15 simple setae; carpus with 6–8 simple setae; propodus with 31–35 simple setae, distal upper extremity corneous; dactyl length about half palm + propodal prolongation, with 24–26 simple setae and distal extremity corneous.

Second pereopod (Fig. 5b, b'): coxa with 7–8 simple setae; basis smaller with 2–3 simple setae; ischium with 8–9 simple setae; merus, longest segment, with 14–16 simple setae; carpus less than half the ischium length, with 11–12 simple setae; propodus longer than carpus, with 23–25 simple setae and 1 stout cuspidate seta; dactylus very stout, apically curved and corneous, with 28–30 simple setae and 3 spines.

Third pereopod (Fig. 5c): coxa with 6–7 simple setae; basis with 3 simple setae and 1 tooth; ischium with 9–11 simple setae; merus longer than ischium and with 14–15 simple setae; carpus with 12–13 simple setae; propodus longer than carpus, with 23–24 simple setae and 1 stout cuspidate seta; dactylus very stout, apically curved and corneous, with 24–26 simple setae and 3 spines.

Fourth pereopod (Fig. 5d, d'): basis with 5–7 simple setae; ischium with 5–8 simple setae; merus with 8–9 simple setae; carpus with 5 simple setae; propodus not chelate with 9 simple setae and 14–16 pseudochaetae as figured; dactyl with 1 long papposerrate seta, 8–9 simple setae and 2 teeth on the distal extremity.

Fifth pereopod (Fig. 5e, e'): coxa with 6–7 simple setae; basis with 3 simple setae; ischium with 2–3 simple setae;

merus with 2 long papposerrate setae and 6–7 small simple setae; carpus with 3 papposerrate and 5–6 simple setae; propodus not chelate with 3 long papposerrate, 16–18 simple setae and 17–18 pseudochaetae as figured; dactyl with 9–11 simple setae and 3–4 spatulate-shaped pseudochaetae distributed as figured.

Abdomen (Fig. 4a): somites with posterolateral angles rounded; somite 1 with 2 pairs of dorsal simple setae, somites 2–3 each with 4 pairs of dorsal simple setae and 3 pairs of simple setae on dorso-lateral margin, somites 4–5 each with 5 pairs of dorsal simple setae and 4–5 pairs of simple setae on dorso-lateral margin, somite 6 with 5 pairs of dorsal simple setae and 7 pairs of simple setae on dorso-lateral margin.

Pleopods (Fig. 5f–i): well developed, biramous, decreasing in size posteriorly; outer ramus with 8–9 plumose setae; inner ramus shorter, with 2 small apical hooks.

Uropods (Fig. 5j): right pair slightly longer than left pair; protopod with 1 simple seta on outer margin; exopod with 4–5 simple setae dorsally, 3–4 simple setae on dorsal margin, 17–19 plumose setae and 10–13 pseudochaetae marginally; endopod with 4–5 simple setae dorsally, 4 simple setae on dorsal margin, 10–11 plumose setae and 7–8 pseudochaetae marginally.

Telson (Fig. 5j): telson with terminal margin rounded, 10–11 pairs of simple setae on the dorsal surface, 2 pairs of pappose setae on the lateral margin and 5–6 pairs of long plumose setae on the distal margin, distributed as illustrated. One of the observed individuals presented an unpaired number (11) of plumose setae.

Clibanarius erythropus (Latreille, 1818) (Fig. 6)

Larval references: Pike and Williamson, 1960: p. 503, Fig. 2 (zoea I, zoea II and zoea III); Le Roux, 1966: p. 227, Fig. 1 (zoea IV); Dechancé and Forest, 1958: p. 277, Fig. 2; p. 283, Figs. 16–23; p. 284, Figs. 24–29 (megalopa)

First zoea (Figs. 6a–j')

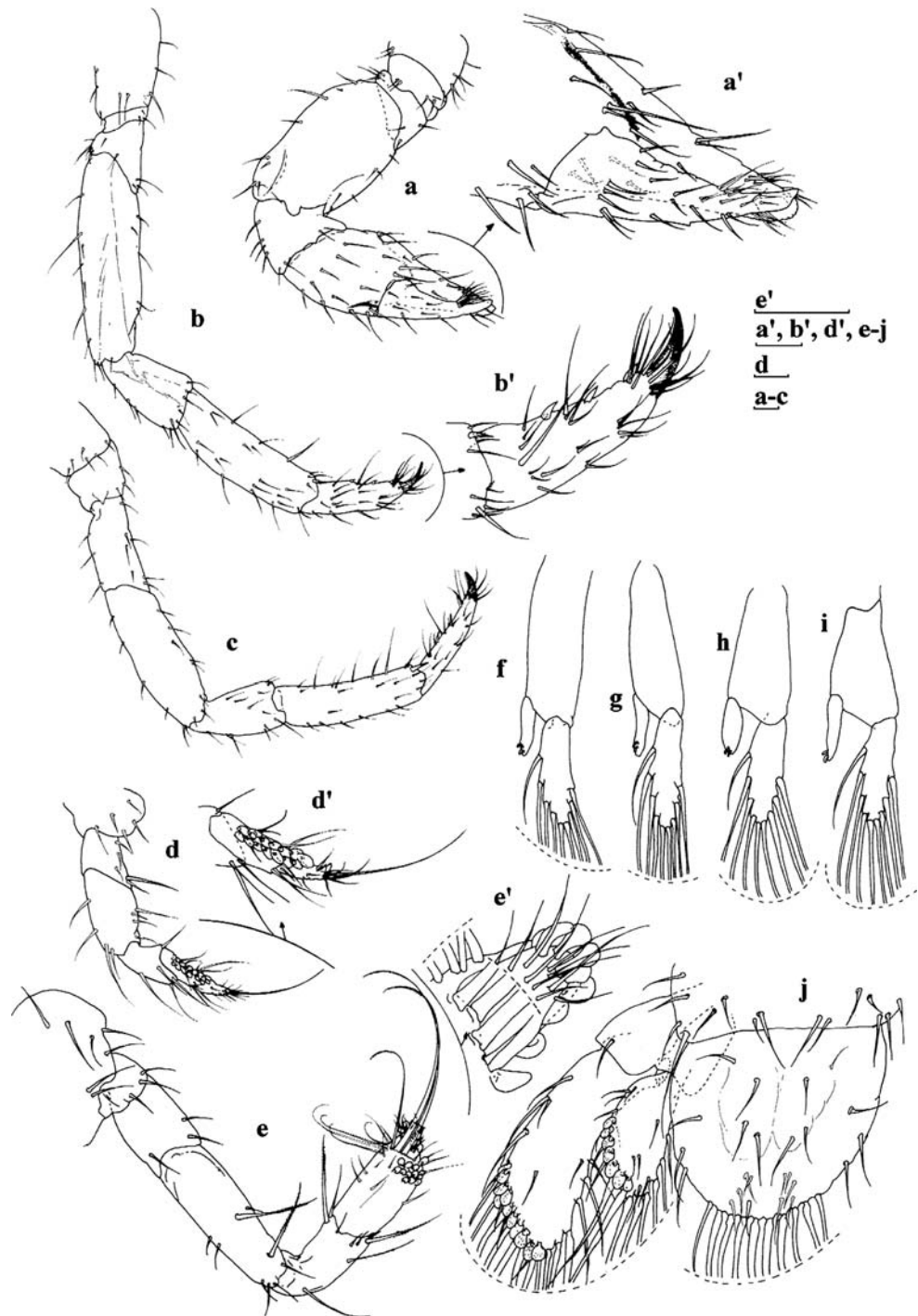
Dimension: TL = 1.83–1.94 mm; CL = 0.81–0.91 mm; R = 0.27–0.38 mm

Carapace (Figs. 6a, a'): without processes or spines, with the postero-lateral border smoothly rounded; rostrum broad, rather blunt, with triangular pointed tip extending beyond antennal scale, rostrum about 0.66 ± 0.08 times the carapace; eyes compound and sessile.

Antennule (Fig. 6b): peduncle unsegmented, with 1 long plumose seta sub-terminally, 3 aesthetascs and 3 unequal simple setae terminally.

Antenna (Fig. 6c): protopod unsegmented with 1 small strong cuspidate seta; endopod with more than half-length

Fig. 5 *Clibanarius aequabilis*. Megalopa: **a** first pereopod; **a'** detail of chela of first pereopod; **b** second pereopod; **b'** detail of dactylus of second pereopod; **c** third pereopod; **d** fourth pereopod; **d'** detail of dactylus of fourth pereopod; **e** fifth pereopod; **e'** detail of propodus and dactylus of fifth pereopod; **f–i** pleopods of abdominal somites 2–5; **j** telson and uropods. Scale bars 0.1 mm (**a–e, f–j**); 0.05 mm (**e'**)



the scale, with 3 long plumose seta apically; scaphocerite unsegmented, with 11 plumose setae.

Mandible (Fig. 6d): asymmetrical; palp absent.

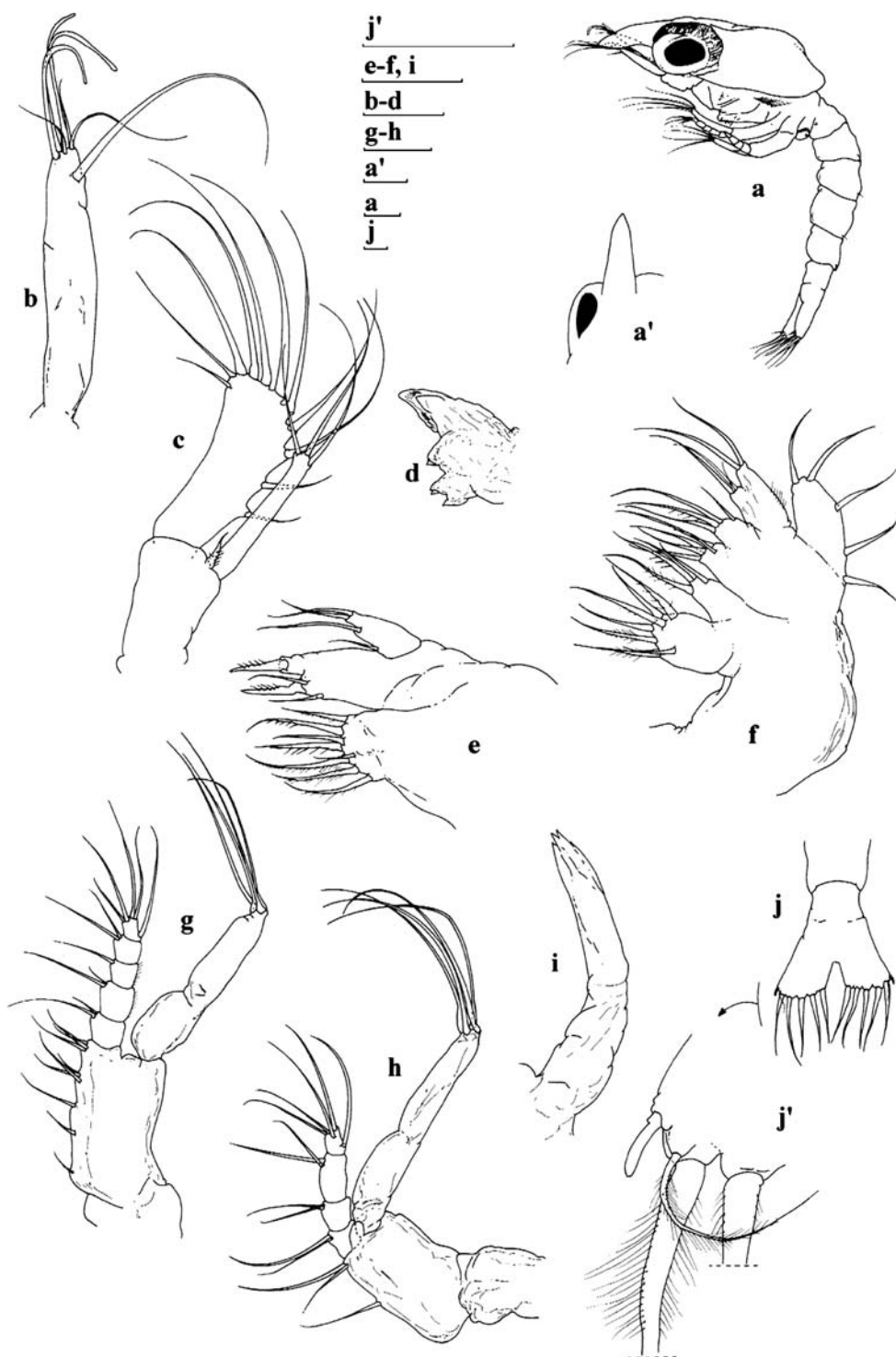
Maxillule (Fig. 6e): coxal endite with 3 serrulate, 2–3 pappose and 2 simple setae, basal endite with 2 cuspidate setae and 2 simple setae; endopod with 1 + 1 + 2 simple setae.

Maxilla (Fig. 6f): coxal endite bilobed with 7–8 + 4 serrulate and papposerrate setae, basal endite bilobed with

5 + 4–5 papposerrate and simple setae; endopod unsegmented bilobed terminally, bearing 3+2 long simple setae and microtricha on outer margin; scaphognathite with 5 marginal plumose setae.

First maxilliped (Fig. 6g): coxa unarmed; basis with 1 + 1 + 1 + 3 + 3 papposerrate setae; endopod 5-segmented with 2, 2, 1, 2 papposerrate and 1+4 papposerrate setae, microtricha on outer margin of second and third segments; exopod unsegmented, with 4 long plumose setae terminally.

Fig. 6 *Clibanarius erythropus*. First zoea: **a** total animal, lateral view; **a'** detail of rostrum, dorsal view; **b** antennule; **c** antenna; **d** mandible; **e** maxillule; **f** maxilla; **g** first maxilliped; **h** second maxilliped; **i** third maxilliped; **j** telson; **j'** detail of posterior margin of telson. Scale bars 1.0 mm (**a'**); 0.1 mm (**a–j'**)



Second maxilliped (Fig. 6h): coxa unarmed; basis with 1 + 2 papposerrate setae; endopod 4-segmented with 2, 2, 2 papposerrate and 1 + 4 papposerrate setae terminally. Exopod unsegmented, with 4 long plumose setae terminally.

Third maxilliped (Fig. 6i): long uniramous bud.

Pereiopods: absent.

Abdomen (Fig. 6a): somites with margins rounded, with a pair of dorso-lateral marginal minute setae on somites 2–5; sixth somite feebly segmented.

Pleopods and uropods: absent.

Telson (Fig. 6j, j'): triangular, broader posteriorly with deep median cleft; with 7 + 7 processes, the first process is a very short blunt spine, the second process an anomuran

hair, the third to the seventh processes plumose setae, being the fourth the longest.

Second zoea

Dimension: TL = 2.10–2.26 mm; CL = 1.02–1.13 mm; R = 0.43–0.48 mm

Carapace: eyes stalked; otherwise unchanged.

Antennule: peduncle unsegmented with 2 long plumose setae sub-terminally and 2 short simple setae terminally, 1 long plumose seta at site of future endopod; exopod bud clearly delineated, with 3 simple setae and 3 aesthetascs.

Antenna: unchanged except for size.

Mandible: molar process with several small denticles and without teeth; otherwise unchanged.

Maxillule: basal endite with 4 cuspidate setae and 2 simple setae; otherwise unchanged except for size.

Maxilla: basal endite bilobed with 5 + 4 papposerrate and simple setae; scaphognathite with 7 marginal plumose setae; otherwise unchanged except for size.

First maxilliped: endopod 5-segmented with 1 + 2, 2–3, 2, 2 papposerrate and 1 + 4 papposerrate setae. Exopod bearing 6 long plumose setae terminally; otherwise unchanged.

Second maxilliped: endopod four-segmented with 2, 2 + 1, 1 + 2 papposerrate and 1 + 4 papposerrate setae terminally. Exopod bearing 6 long plumose setae terminally; otherwise unchanged.

Third maxilliped: biramous; endopod represented by a small bud basally situated; exopod unsegmented, bearing 5 plumose setae.

First to third pereopods: present as small uniramous buds.

Abdomen: unchanged except for size.

Pleopods and uropods: absent.

Telson: 8 + 8 processes, with an additional inner pair of telson plumose setae; broader posteriorly with the median cleft less pronounced; otherwise unchanged.

Third zoea

Dimension: TL = 2.74–2.85 mm; CL = 1.35–1.51 mm; R = 0.48–0.59 mm

Carapace: unchanged except for size.

Antennule: peduncle unsegmented with 1 small basal simple seta, 4 long plumose setae and 4 short simple setae distally; the outer flagellum with 3 aesthetascs, 1 long plumose seta and 3 shorter simple setae; the inner flagellum small, bud-like.

Antenna: endopod as long as the scale, with 1 short plumose seta in apical region; scaphocerite with 11–12 plumose setae. Otherwise unchanged.

Mandible and maxillule: unchanged except for size.

Maxilla: coxal endite bilobed with 8 + 4 serrulate and papposerrate setae; scaphognathite with 9–10 marginal plumose setae; otherwise unchanged except for size.

First and second maxillipeds: unchanged except for size.

Third maxilliped: endopod bud enlarged in size; exopod unsegmented, bearing 6 plumose setae.

First pereopod: uniramous bud showing its chelate nature.

Second and third pereopods: unchanged except for size.

Fourth and fifth pereopods: small uniramous buds.

Abdomen: abdominal somite 6 fully separated from telson, bearing a pair of dorso-lateral marginal minute setae on somites 2–5; otherwise unchanged.

Pleopods: absent.

Uropods: biramous; exopod well developed, not reaching the end of telson, with 7–8 plumose setae; endopod a small bud with 2 minute projections at its tip.

Telson: triangular, broader posteriorly with the median cleft less pronounced; the number of telson processes: 8–9 + 9 (the first process as a very short blunt spine, the second as an anomuran hair, the third as a plumose seta, the fourth as a very reduced fused spine and the fifth to eighth or ninth processes as plumose setae).

Fourth zoea

Dimension: TL = 3.01–3.17 mm; CL = 1.51–1.61 mm; R = 0.48–0.59 mm

Carapace: unchanged except for size.

Antennule: peduncle unsegmented with 2 simple setae on lateral margin, 4 short simple and 4 long plumose setae distally; outer flagellum with 2 + 2 + 2 + 1 aesthetascs, 2 long and 2 short plumose setae; inner flagellum unsegmented, enlarged in size.

Antenna: endopod longer than antennal scale, two-segmented: first segment unarmed, second segment with a short plumose seta and a pointed tip terminally; scaphocerite with 11–13 plumose setae. Otherwise unchanged.

Mandible: presence of an unsegmented palp.

Maxillule: unchanged except for size.

Maxilla: coxal endite bilobed with 9–12 + 4 serrulate and papposerrate setae; basal endite with 6–7 + 4–5 papposerrate and simple setae; endopod unsegmented, bilobed, terminally bearing 3 + 2 long simple setae; scaphognathite with 13–16 marginal plumose setae.

First and second maxillipeds: unchanged.

Third maxilliped: endopod two-segmented, incomplete 2 to 5 segments with two-minute projection at its tip; otherwise unchanged.

First pereopod: cheliped with chela enlarged, dactyl distinct, coxa and merus clearly delineated, with tubercles on surface.

Second and third pereopods: long, six segments clearly delineated, coxa and merus with some tubercles on surface.

Fourth and fifth pereopods: short, with some segments clearly delineated.

Abdomen: unchanged except for size.

Pleopods: present as biramous buds on segments 2 to 5.

Uropods: total individualization of protopod, exopod and endopod; exopod with 9–10 plumose setae on apical region and 2–3 papposerrate setae on ventral surface; endopod smaller, with 4–5 plumose setae on apical region and 1 pappose seta on ventral surface.

Telson: almost rectangular in shape; number of telson processes: 9 + 9 (first process as a very short blunt spine, second as an anomuran hair, third as a plumose seta, fourth as a very reduced fused spine and fifth to ninth processes as plumose setae).

Megalopa

Dimension: TL = 2.80–2.96 mm; CL = 1.08–1.24 mm; R = 0.16–0.22 mm

Carapace: smooth, slightly broader than long; rostrum broad and blunt; ocular peduncles stout, reaching the end of the antennular peduncle; ocular acicles not developed; surface and margins with proboscate setae distributed as figured.

Antennule: peduncle three-segmented, proximal segment with 2 papposerrate, 4–6 simple and 5 papposerrate setae; second segment with 1 long and 3–5 short simple setae and 1 papposerrate seta; distal segment with 5–6 simple setae; outer flagellum five-segmented, proximal segment unarmed, second segment with 5 aesthetascs, third segment with 5 aesthetascs and 4–5 simple setae, fourth segment with 3 aesthetascs and 2–3 simple setae terminally, distal segment with 3–4 simple setae; inner flagellum three-segmented with 2, 2–3 and 6–8 simple setae.

Antenna: basis with 3 simple setae, peduncle 3-segmented with 1–2, 2, 4–5 simple setae; flagellum composed of 9–10 segments, each with 0–6 simple setae on distal margin, except for the distal segment which has 8–9 simple setae on distal margin; acicle with 1 spine-like projection on lateral margin, 4 simple setae and bifid spinous tip.

Mandibles: reduced and simplified, lower extremities of the incisor part with processes as illustrated; palp three-segmented, proximal segment with 1 strong simple seta,

second segment unarmed, distal segment with 4–5 simple setae and 4–5 serrulate setae terminally.

Maxillule: coxa with 18–20 papposerrate and simple setae; basis with 2 simple setae on lateral inner margin and 5 cuspidate, 5 serrulate, 6–7 papposerrate, 3 simple and 1 long plumose setae on distal margin; endopod unsegmented with 1 + 1 simple setae; 1 plumose seta present on inner margin of basis.

Maxilla: coxa bilobed with 27–29 + 7–8 papposerrate and simple setae; basis bilobed with 9–12 + 10–13 papposerrate and simple setae; endopod unsegmented without seta; scaphognathite with 47–52 plumose setae on distal margin and 1 simple seta on dorsal surface of the upper lobe.

First maxilliped: coxa with 2–3 simple, 2–3 pappose and 3 papposerrate setae; basis with 3–4 simple, 3 serrulate and 13–14 papposerrate setae; unsegmented endopod without seta; exopod unsegmented with 6–8 plumose setae on outer margin.

Second maxilliped: coxa without any seta or with 1 simple seta; basis with 2–3 pappose setae; endopod four-segmented, proximal segment with 1 + 1 simple setae, second segment with 2–3 simple setae, third segment with 7–9 simple and papposerrate setae, and 6–7 papposerrate setae on distal segment; exopod two-segmented with 2 simple setae on proximal segment and 8 plumose setae terminally on distal segment.

Third maxilliped: basis with 5–7 simple setae and 3–4 sub-acute processes; endopod five-segmented, ischium with 7–9 simple seta and 4–5 sub-acute processes on *crista dentata*, merus with 4–6 simple setae, carpus with 9–10 simple setae, propodus with 3–4 simple, 2 cuspidate and 13–15 papposerrate setae, and dactyl with 5 serrate, 6–7 simple, 3 cuspidate and 5–6 papposerrate setae; exopod 2-segmented with 1 simple seta on proximal segment and 8 plumose setae terminally on distal segment.

First pereopod: chelae equal, with segments smooth; coxa with 9–10 simple setae; basis with 4 simple setae; ischium with 8–9 simple setae; merus, longest segment, with 14–16 simple setae; carpus with 6–7 simple setae; propodus with 38–40 simple setae, distal upper extremity corneous; dactyl length about half palm + propodal prolongation, with 23–26 simple setae and distal extremity corneous.

Second pereopod: coxa with 7–8 simple setae; basis smaller with 2 simple setae; ischium with 7–8 simple setae; merus, longest segment, with 14–16 simple setae; carpus less than half the ischium length, with 12–14 simple setae; propodus longer than carpus, with 22–25 simple setae and 1 stout cuspidate seta; dactylus very stout, apically curved and corneous, with 27–29 simple setae and 3–4 spines.

Third pereopod: coxa with 7–8 simple setae; basis with 4–5 simple setae; ischium with 10–11 simple setae; merus

longer than ischium and with 14–16 simple setae; carpus with 11–12 simple setae; propodus longer than carpus, with 24–27 simple setae and 1 stout cuspidate seta; dactylus very stout, apically curved and corneous, with 25–28 simple setae and 3–4 spines.

Fourth pereopod: basis with 7 simple setae; ischium with 8–10 simple setae; merus with 9–10 simple setae; carpus with 4–5 simple setae; propodus not chelate, with 8–9 simple setae and 10–14 pseudochaetae; dactyl with 1 long papposerrate seta, 7–9 simple setae and 2 teeth on distal extremity.

Fifth pereopod: coxa with 5–6 simple setae; basis with 3 simple setae; ischium with 2–3 simple setae; merus with 2 long papposerrate setae and 6–7 small simple setae; carpus with 3 papposerrate and 5–6 simple setae; propodus not chelate, with 5–6 long papposerrate, 16–18 simple setae and 11–13 pseudochaetae; dactyl with 5–7 simple setae and 3 spatulate-shaped pseudochaetae.

Abdomen: somites with posterolateral angles rounded; somite 1 with 2 pairs of dorsal simple setae, somites 2–3 each with 4–5 pairs of dorsal simple setae and 5 pairs of simple setae on dorsolateral margin, somites 4–5 each with 5 pairs of dorsal simple setae and 4–5 pairs of simple setae on dorsolateral margin, somite 6 with 5 pairs of dorsal simple setae and 6 pairs of simple setae on dorsolateral margin.

Pleopods: well developed, biramous, decreasing in size posteriorly; outer ramus with 8–9 plumose setae; inner ramus shorter, with 2 small apical hooks.

Uropods: right one slightly longer than left one; protopod with 4 simple setae on outer margin; exopod with 3 simple setae dorsally, 4 simple setae on dorsal margin, 16–18 plumose setae and 9–11 pseudochaetae marginally; endopod with 3–5 simple setae dorsally, 4–5 simple setae on dorsal margin, 8–9 plumose setae and 5–8 pseudochaetae marginally.

Telson: telson with terminal margin rounded, 8–9 pairs of simple setae on dorsal surface, 2 pairs of pappose setae on lateral margin and 5 pairs of long plumose setae on the distal margin.

Discussion

Larval stages of *C. erythropus* cultured in the present study displayed only minor differences to those described previously by Pike and Williamson (1960), Le Roux (1966) and Dehancé and Forest (1958). In our study the first zoeal stage had longer TL and CL than described by Pike and Williamson (1960) and Le Roux (1966), while the megalopa was smaller than recorded by Dehancé and Forest (1958) (Table 1). In the first zoeal stage, the endopod of the maxillule was found unsegmented, whereas in

previous studies it had been described as a two-segmented structure. Although Pike and Williamson (1960) and Le Roux (1966) reported the absence of pereopods in the second zoeal stage, in our study this zoeal stage already presented the first three pairs of pereopods as small buds. No significant differences were found in the third zoeal stage, but in zoea IV the segmentation of the third maxilliped differed between our specimens and those previously described (see Table 1). The differences in setation patterns may result from different geographical origins of ovigerous females. In our study and in that of Le Roux (1966), ovigerous females were collected in the coastal waters of the northeastern Atlantic (in Ria do Alvor, Algarve, Portugal and in Île Bailleron, Bretagne, France, respectively), while those used by Pike and Williamson (1960) and Dehancé and Forest (1958) originated from the Mediterranean Sea (Naples, Campania region, Italy and Banyuls-sur-Mer, Languedoc-Roussillon region, France, respectively). Similar intra-specific variations were recorded and discussed by Siddiqui et al. (1991), when comparing larval series of *C. antillensis* from Panamanian and Brazilian populations.

The larval stages of the two northeastern Atlantic *Clibanarius* species, *C. aequabilis* and *C. erythropus*, cannot be easily differentiated (Table 1). However, the zoeal stages of *C. aequabilis* were always 23–30% bigger than those of *C. erythropus*. Besides size, there were only small differences (Table 1). In the megalopa stage, *C. aequabilis* can be distinguished from *C. erythropus* by the number of segments of the mandibular palp: 2 segments in *C. aequabilis* and 3 in *C. erythropus*.

Table 1 summarizes the available data on morphological larval characters of *Clibanarius* species. Concerning larval morphology, the genus *Clibanarius* is very homogeneous and available data allow us to complete Shenoy and Sankolli's (1977) definition of its generic larval features. Thus, *Clibanarius* zoeae have a smooth and rounded carapace with a broad and blunt rostrum; the abdominal segments are also smooth, and dorso-marginal spines are missing. The antennal scale lacks a terminal spine; the eyes are stalked in the second larval stage, with rounded eyes at the top of a short ocular peduncle. From the third zoeal stage on, the formula of the telson processes is usually $8 + 1 + 8$, but also $9 + 9$ or $9 + 9 - 10$; the outermost process is a very short blunt spine, the second an anomuran hair, the third an articulated plumose seta, the fourth a fused spine (reduced or well developed), and the fifth to ninth or tenth processes are plumose setae. Biramous uropods are already present in the third stage, and in the fourth stage the mandibular palp is present. *Clibanarius* megalopa displays a carapace without processes or spines, with the postero-lateral border smoothly rounded, and a broad and rather blunt rostrum; the abdominal somites have their

Table 1 Comparison of relevant larval characters of *Citbanarius* species

Features	<i>C. acqualilis</i> (present study)	<i>C. erythropus</i> (1), (2), (3)	<i>C. antillensis</i> (4)	<i>C. vittatus</i> (5)	<i>C. scleripetarius</i> (6)	<i>C. albidigitus</i> (7)	<i>C. signatus</i> (8)	<i>C. virens</i> (8)	<i>C. infraspinatus</i> (9)	<i>C. merguensis</i> (10)	<i>C. padavensis</i> (11)	<i>C. citbanarius</i> (12)	<i>C. longitarsus</i> (13)	<i>C. olivaceus</i> (14)
Females collection area	NE Atlantic	NE Atlantic	Caribbean Sea	NW Atlantic	SW Atlantic	Central E Pacific	Arabian Sea	Arabian Sea	Arabian Sea	Arabian Sea	Arabian Sea	Bay of Bengal	Bay of Bengal	Bay of Bengal
Stages: zoea (Z)+megalopa (M)	4Z+1M	4Z+1M	4Z+1M	5Z+1M	5Z+1M	4Z+1M	4Z+1M	4Z+1M	4Z+1M	4Z+1M	4Z+1M	4Z+1M	4Z+1M	5Z+1M
First Zoea														
Total length, mm	2.39-2.62	1.83-1.94	1.20	1.90-2.40	-	-	1.60	1.80	-	-	-	1.90	1.52	1.57
Carapace length, mm	1.04-1.12	0.81-0.91	0.80	0.90-1.10	-	0.63-0.76	-	-	1.00	1.00	-	0.85	0.85	0.90
CARAPACE	0.89±0.06	0.66±0.08	-	-	-	-	-	-	-	-	-	-	-	-
Rostrum/carapace	Unseg./	Unseg./	Unseg./	Unseg./	Unseg./	Unseg./	Unseg./	Unseg./	Unseg./	Unseg./	Unseg./	Unseg./	Unseg./	Unseg./
ANTENNULE	1+(3)+3	1+(3)+3	1+(3)+3	1+(3)+2-3	1+(2)+2	1+(2-4)+2-3	1+(4)+2	1+(4)+1	1+(3)+3	1+(2)+2	1+(2)+3	1+(2)+3	1+	1+(3)+3
Peduncle: segments/ setae	Unseg./	Unseg./	Unseg./	Unseg./	Unseg./	Unseg./	Unseg./	Unseg./	Unseg./	Unseg./	Unseg./	Unseg./	Unseg./	Unseg./
ANTENNA	Unseg./	Unseg./	Unseg./	Unseg./	Unseg./	Unseg./	Unseg./	Unseg./	Unseg./	Unseg./	Unseg./	Unseg./	Unseg./	Unseg./
Protopod: segments/ setae	Unseg./	Unseg./	Unseg./	Unseg./	Unseg./	Unseg./	Unseg./	Unseg./	Unseg./	Unseg./	Unseg./	Unseg./	Unseg./	Unseg./
Endopod: segments/ setae	Unseg./	Unseg./	Unseg./	Unseg./	Unseg./	Unseg./	Unseg./	Unseg./	Unseg./	Unseg./	Unseg./	Unseg./	Unseg./	Unseg./
Scaphocerite	11	11	10-11	9-11	11	11	11	11	11	11	10-11	11	-	11
MAXILLULE	7	7-8	7	6	5	7	7	5	7	6	5	7	-	6
Coxal endite	5	4	4	3-4	3	4	4	2	3	3	3	3	3	3
Endopod: segments/ setae	Unseg./	Unseg./	Unseg./	Unseg./	Unseg./	Unseg./	2/1,2	2/1,2	-	Unseg./	Unseg./	Unseg./	Unseg./	Unseg./
MAXILLA	7+4	7-8+4	7+3	6+4	3+2-3	7+4-5	6+3	5+3	7+4	6+4	7+3	6+3	-	6+3
Coxal endite	5+4	5+4-5	4-5+3	5+3-4	5-6+2-3	5-6+4	5+4	4+4	5+3	4+4	4+3	2+4	-	4+4
Endopod: segments/ setae	Unseg./	Unseg./	Unseg./	Unseg./	Unseg./	Unseg./	Unseg./	Unseg./	Unseg./	Unseg./	Unseg./	Unseg./	Unseg./	Unseg./
Scaphognathite	5	5	5-6	4-6	5	5	5	5	5	5	5	5	5	5
FIRST MAXILLIPED	9	9	6	7-9	7	7-8	6	9	7	8	6-7	-	6	6
Endopod: segments/ setae	5/2,2,2,2,5	5/2,2,1,2,5	5/1,3,2,3,5	5/2,2,1,3,4	5/1,1,1,3,3	5/2,2,1,2,5	5/2,2,2,3,4	-	5/2,2,1,2,5	5/1,2,1,2,5	5/2,2,1,2,5	5/2,2,2,2,5	5/2,2,2,3,4	5/2,2,2,3,4
Exopod: segments/ setae	Unseg./	Unseg./	2/0,4	Unseg./	-	2/0,4	Unseg./	-	Unseg./	2/0,4	Unseg./	Unseg./	Unseg./	Unseg./
SECOND MAXILLIPED	3	3	3	3	3-6	3	3	3	3	4	3	3	-	2
Basial endite	4/2,2,2,5	4/2,2,2,5	4/2,3,3,5	4/2,2,2,5	4/2,2,2,3	4/2,2,2,5	4/2,2,2,5	4/2,2,2,5	4/2,2,2,5	4/2,2,2,5	4/2,2,1,5	4/2,2,2,5	4/2,2,3,4	4/2,2,3,4
Endopod: segments/ setae	Unseg./	Unseg./	2/0,4	Unseg./	-	2/0,4	Unseg./	Unseg./	Unseg./	2/0,4	Unseg./	Unseg./	Unseg./	Unseg./
Exopod: segments/ setae	Unseg./	Unseg./	Unseg./	Unseg./	Unseg./	Unseg./	Unseg./	Unseg./	Unseg./	Unseg./	Unseg./	Unseg./	Unseg./	Unseg./
THIRD MAXILLIPED	Unseg./	Unseg./	Unseg./	Unseg./	Unseg./	Unseg./	Unseg./	Unseg./	Unseg./	Unseg./	Unseg./	Unseg./	Unseg./	Unseg./
Development	Unseg./	Unseg./	Unseg./	Unseg./	Unseg./	Unseg./	Unseg./	Unseg./	Unseg./	Unseg./	Unseg./	Unseg./	Unseg./	Unseg./
Segments	7+7	7+7	7+7	7+7	7+7	7+7	7+7	7+7	7+7	7+7	7+7	7+7	7+7	7+7
Posterior margin processes	7+7	7+7	7+7	7+7	7+7	7+7	7+7	7+7	7+7	7+7	7+7	7+7	7+7	7+7

Table 1 continued

Features	<i>C. aequabilis</i>	<i>C. erythropus</i>	<i>C. erythropus</i>	<i>C. antillensis</i>	<i>C. vittatus</i>	<i>C. scolopetarius</i>	<i>C. albidigatus</i>	<i>C. signatus</i>	<i>C. virescens</i>	<i>C. infuspinatus</i>	<i>C. merguensis</i>	<i>C. paduensis</i>	<i>C. clibanarius</i>	<i>C. longitarsus</i>	<i>C. olivaceus</i>
Second Zoëa															
Total length, mm	3.00–3.23	2.10–2.26	2.00–2.20	1.91–2.00	2.20–2.90	-	-	-	2.20	-	-	2.43	2.21	2.00	
Carapace length, mm	1.31–1.39	1.02–1.13	1.10	1.00–1.02	1.10–1.30	-	0.85–1.20	-	-	1.20	1.20	1.05	1.07	1.08	
Rostrum/ carapace	0.89±0.06	0.72±0.05	-	-	-	-	-	-	-	-	-	-	-	-	
ANTENNULE	Unir/2-seg.	Unir/2-seg.	-	Unir/2-seg.	Unir/2-seg.	Unir/2-seg.	Unir/2-seg.	Unir/2-seg.	Unir/2-seg.	Unir/2-seg.	Unir/2-seg.	Unir/2-seg.	Unir/2-seg.	Unir/2-seg.	
Peduncle: setae	5	5	-	5	3–6	3	4–5	6	6	6–7	3	5	-	3	
Outer flagellum: setae	3+(3)	3+(3)	-	3+(5)	2–3+(4)	3+(2)	3–4+(3–4)	1+(5)	2+(4)	6+(1)	3+(2)	4+(2)	-	2+(4)	
ANTENNA	11	11	10–12	10–11	11	12	11–12	12	11	11	11	12	-	-	
Scaphocerite	Unseg./4	Unseg./4	-	Unseg./3	Unseg./3–4	Unseg./3	Unseg./4	2/1,2	-	Unseg./3	Unseg./3	Unseg./3	Unseg./-	Unseg./3	
Endopod: segments/ setae	7	7	-	6–7	7	7	7	6	6	6	6–7	6–7	8	7	
MAXILLULE	Unseg./6	Unseg./6	Unseg./6	20/6	Unseg./6	-/6	20/6	Unseg./6	Unseg./6	Unseg./6	20/6	Unseg./6	Unseg./6	Unseg./6	
FIRST MAXILLIPED	Unseg./6	Unseg./6	Unseg./6	20/6	Unseg./6	-/6	20/6	-	Unseg./6	Unseg./6	20/6	Unseg./6	Unseg./6	Unseg./6	
Exopod: segments/ setae	Bud	Bud	Bud	Bud	Absent	-	Bud	Absent	Bud	Bud	Bud	Bud	Bud	Bud	
SECOND MAXILLIPED	Unseg./6	Unseg./5	Unseg./4–5	20/5	-/4–5	-/5	2/0,5–6	Unseg./4	Unseg./5	Unseg./5	Unseg./5	Unseg./5	Unseg./5	Unseg./5	
Exopod: segments/ setae	1–3 unir. buds	1–3 unir. buds	Absent	-	-	-	-	-	-	-	-	-	-	-	
THIRD MAXILLIPED	5 somites	5 somites	5–6 somites	5 somites	-	5 somites	5 somites	-	-	5 somites	5 somites	5 somites	6 somites	6 somites	
Endopod: development	8+8	8+8	8+8	8+8	8+8	8+8	8+8	8+8	8+8	8+8	8+8	8+8	8+8	8+8	
Exopod: segments/ setae	8+8	8+8	8+8	8+8	8+8	8+8	8+8	8+8	8+8	8+8	8+8	8+8	8+8	8+8	
PEREIOPODS	8+8	8+8	8+8	8+8	8+8	8+8	8+8	8+8	8+8	8+8	8+8	8+8	8+8	8+8	
ABDOMEN	8+8	8+8	8+8	8+8	8+8	8+8	8+8	8+8	8+8	8+8	8+8	8+8	8+8	8+8	
TELSON	8+8	8+8	8+8	8+8	8+8	8+8	8+8	8+8	8+8	8+8	8+8	8+8	8+8	8+8	
Posterior margin processes	8+8	8+8	8+8	8+8	8+8	8+8	8+8	8+8	8+8	8+8	8+8	8+8	8+8	8+8	
Third Zoëa															
Total length, mm	3.44–3.77	2.74–2.85	2.80	2.90–3.20	2.80–4.10	-	-	2.10	2.50	-	-	2.96	2.95	2.43	
Carapace length, mm	1.61–1.72	1.35–1.51	1.40	1.50–1.70	1.50–2.00	-	1.20–1.40	-	-	1.50	1.40	1.33	1.43	1.20	
CARAPACE	0.86±0.03	0.60±0.04	-	-	-	-	-	-	-	-	-	-	-	-	
Rostrum/ carapace	Biram.	Biram.	-	Unir/2-seg.	Unir/2-seg.	Biram.	Biram.	Biram.	Biram.	Biram.	Biram.	Biram.	Biram.	Biram.	
ANTENNULE	4+(3)	4+(3)	-	-/4(5)	5+(2)	3+(2)	3–4+(2–4)	2+(4)	1+(5)	6+(1)	4+(3)	4+(2)	-	4+(4)	
Outer flagellum: setae	Small (bud)	Small (bud)	-	Absent	Absent	Small (bud)	Small (bud)	Small (bud)	Small (bud)	Small (bud)	Small (bud)	Small (bud)	Small (bud)	Small (bud)	
Inner flagellum: development	12	11–12	10–12	12	11–12	11–12	12	12	12	12	12	12	12	12	
ANTENNA	10–11	9–10	-	10–13	7–10	10–11	9–11	8	11	12–13	10	10	9	9	
Scaphocerite	Bud	Bud	Bud	3-seg. bud	Absent	Bud	Bud	Bud	Bud	Bud	Bud	Bud	Bud	Bud	
MAXILLA	Unseg./6	Unseg./6	Unseg./4–5	20/5	20/5–6	-	2/0,5–6	Unseg./6	Unseg./6	Unseg./6	Unseg./6	Unseg./6	Unseg./6	Unseg./6	
THIRD MAXILLIPED	Unseg./6	Unseg./6	Unseg./4–5	-	-	-	Buds	All as buds	All as buds	Unseg./6	Unseg./6	Unseg./6	Unseg./6	Unseg./6	
Endopod: development	All as buds	All as buds	All as buds	-	-	-	Biram.	Biram.	Biram.	Biram.	Biram.	Biram.	Biram.	Biram.	
Exopod: segments/ setae	7–8	7–8	6–7	8	6–9	7	6–8	7–8	-	8–9	8	8–9	8	7	
PEREIOPODS	9+10	8+9	8+8	8+1+8	8+1+8	8+1+8	8+1+8	8+1+8	8+1+8	8+1+8	8+1+8	8+1+8	8+1+8	8+1+8	
UROPODS	Reduced	Reduced	Reduced	Well developed	Well developed	Reduced	Well developed	Reduced	Well developed	Reduced	Well developed	Reduced	Reduced	Reduced	
TELSON	9+10	8+9	8+8	8+1+8	8+1+8	8+1+8	8+1+8	8+1+8	8+1+8	8+1+8	8+1+8	8+1+8	8+1+8	8+1+8	
Posterior margin processes	9+10	8+9	8+8	8+1+8	8+1+8	8+1+8	8+1+8	8+1+8	8+1+8	8+1+8	8+1+8	8+1+8	8+1+8	8+1+8	
4 th telson process: fused spine	Reduced	Reduced	Reduced	Well developed	Well developed	Reduced	Well developed	Reduced	Well developed	Reduced	Well developed	Reduced	Reduced	Reduced	

Table 1 continued

Features	<i>C. aequabilis</i>	<i>C. erythropus</i>	<i>C. antillensis</i>	<i>C. vittatus</i>	<i>C. sclopetarius</i>	<i>C. albidigius</i>	<i>C. signatus</i>	<i>C. virescens</i>	<i>C. infraspinatus</i>	<i>C. merguensis</i>	<i>C. clibanarius</i>	<i>C. longiurus</i>	<i>C. olivaceus</i>
Fourth Zoëa													
Total length, mm	4.08-4.40	3.01-3.17	3.10-3.30	3.60-5.20	-	-	-	3.80	-	-	3.77	3.58	3.19
Carpapace length, mm	1.92-2.08	1.51-1.61	1.60-1.70	1.70-2.60	-	1.50-1.70	-	-	1.60	1.70	1.72	1.63	1.73
CARPAPACE													
Rostrum/ canapace	0.86±0.08	0.54±0.04	-	-	-	-	-	-	-	-	-	-	-
ANTENNULE													
Outer flagellum: segments/setae	Unseg./4+(7)	Unseg./4+(7)	Unseg./4+(9)	Unseg./4+(4-5)	Unseg./4-5+(4-5)	Unseg./3-4+(7)	Unseg./2+(6)	Unseg./1+(7)	Unseg./6+(1)	Unseg./4+(3)	Unseg./9+(+)	Unseg./-	Unseg./4+(4)
Inner flagellum: development	Unseg./0	Unseg./0	Unseg./0	Bud	Unseg./0	Unseg./0	Unseg./1	Unseg./0	Unseg./0	Unseg./2	Unseg./0	Unseg./0	Unseg./0
ANTENNA													
Scaphocerite	12-13	11-13	13	11-14	12-13	11-12	10	12	-	13	14	13	13
MANDIBLE	Palp present	Palp present	Palp present	Palp present/Absent	Palp present	Palp present	Palp present	Palp present	Palp present	Palp present	Palp present	Palp present	Palp present
MAXILLA													
Endopod: segments/setae	Unseg./3+2	Unseg./3+2	Unseg./2+2	Unseg./2+2	Unseg./2+2	Unseg./2+2	Unseg./4	Unseg./4	-	Unseg./2+2	Unseg./2+2	Unseg./-	Unseg./2+2
Scaphognathite	15-17	13-16	12-16	12-14	12	12-18	9	16	-	14	13	13	16
FIRST MAXILLIPED													
Exopod: segments/setae	Unseg./6	Unseg./6	2/0,6	Unseg./6	-/7	Unseg./6-7	Unseg./6	Unseg./6	Unseg./6	20,6	Unseg./7	Unseg./6	-
SECOND MAXILLIPED													
Exopod: segments/setae	Unseg./6	Unseg./6	2/0,6	Unseg./6-7	-/7	Unseg./7-8	Unseg./6	Unseg./6	Unseg./6	20,6	Unseg./7	Unseg./6	-
THIRD MAXILLIPED													
Endopod: development	2-seg	2-seg	Inc. 5-seg	Absent	Unseg.	Inc. 3-5 seg.	-	Unseg.	-	3-seg.	Unseg.	Unseg.	Unseg.
Exopod: segments/setae	Unseg./6	Unseg./6	2/0,5	20,5-6	-/6	2/0,5-6	-	Unseg./6	Unseg./6	Unseg./6	Unseg./7	Unseg./6	Unseg./6
PEREOPODS	All as buds	All as buds	All as buds	All as buds	-	All as buds	All as buds	All as buds	-	All as buds	All as buds	All as buds	All as buds
PLEOPODS	Biram. buds	Biram. buds	Biram. buds	Absent-small buds	Biram. buds	Biram. buds	Biram. buds	Biram. buds	Biram. buds	Biram. buds	Biram. buds	Biram. buds	Absent
UROPODS													
Uropod endopod: marginal setae	5	4-5	5-6	3-6	4-5	4-6	4	4	-	4-6	5	5	5
Uropod exopod: marginal setae	8-9	9-10	10	6-9	9-11	8-10	9	9	-	9-10	12	11	11
TELSON													
Posterior margin processes	9+9-10	9+9	8+1+8	8+1+8/9+9	8+1+8	8+1+8	8+1+7	8+1+8	8+1+8	8+1+8	8+1+8	8+1+8	8+1+8
4 th telson process: fused spine	Reduced	Reduced	Well developed	Well developed	Reduced	Well developed	Reduced	Well developed	Reduced	Well developed	Reduced	Reduced	Reduced
Fifth Zoëa													
Total length, mm	-	-	-	4.30-5.30	-	-	-	-	-	-	-	-	3.76
Carpapace length, mm	-	-	-	2.30-2.70	-	-	-	-	-	-	-	-	2.19
ANTENNULE													
Inner flagellum: development	-	-	-	Unseg./0-1	Unseg./0	-	-	-	-	-	-	-	Unseg./1
ANTENNA													
Endopod: segments/setae	-	-	-	2/0,1	3/0,0,1	-	-	-	-	-	-	-	-
MANDIBLE	-	-	-	Palp present	2-seg. palp	-	-	-	-	-	-	-	Unseg. palp
SECOND MAXILLIPED	-	-	-	Unseg./8	-/7	-	-	-	-	-	-	-	-
Exopod: segments/setae	-	-	-	Bud	Unseg.	-	-	-	-	-	-	-	-
THIRD MAXILLIPED	-	-	-	2/0,6	-/6	-	-	-	-	-	-	-	Unseg.
Endopod: development	-	-	-	All as buds	Biram. buds	-	-	-	-	-	-	-	Unseg./7
Exopod: segments/setae	-	-	-	Unir. buds	Biram. buds	-	-	-	-	-	-	-	All as buds
PEREOPODS	-	-	-	9+9	8+1+8	-	-	-	-	-	-	-	Biram. buds
PLEOPODS	-	-	-										
TELSON	-	-	-										
Posterior margin processes	-	-	-										8+1+8

Table 1 continued

Features	<i>C. acqualibis</i>	<i>C. erythropus</i>	<i>C. erythropus</i>	<i>C. antillensis</i>	<i>C. vittatus</i>	<i>C. scolopetarius</i>	<i>C. albigatus</i>	<i>C. signatus</i>	<i>C. virescens</i>	<i>C. infuspinatus</i>	<i>C. merguensis</i>	<i>C. padavensis</i>	<i>C. clibanarius</i>	<i>C. longitarsus</i>	<i>C. olivaceus</i>
Megalopa															
Total length, mm	2.85-3.04	2.80-2.96	3.10-3.30	2.70-2.90	3.20-4.10	-	-	2.50	3.20	-	-	-	2.72	3.14	3.40
Carapace length, mm	1.08-1.15	1.08-1.24	0.90-1.00	0.60-0.80	1.10-1.50	-	-	0.80-1.00	-	1.40	1.20	1.20	1.12	1.09	1.34
CARAPACE															
Rostrum	Broad, blunt	Broad, blunt	Broad, blunt	Triangular	Small, blunt	Small, blunt	Broad, blunt	Triangular	Truncated	-	Broad	Triangular	Broad, rounded	Broad, rounded	Broad, rounded
Rostrum/carapace	0.17±0.02	0.18±0.03	-	-	-	-	-	-	-	-	-	-	-	-	-
Ocular scales	Absent	Absent	Absent	-	Absent	-	-	-	-	-	-	-	-	-	-
ANTENNULE															
Peduncle: segments/ setae	3/12-13-4-5-6	3/11-13-5-7-5-6	3/-	3/7-1-2-1-2	-	3/9-13-,-	3/7-10-3-5-5-5	3/-	3/-	3/-	3/-	3/-	3/-	3/-	3/-
Outer flagellum: segments/ aesthetascs	5/	5/	5/	5/	5/	5/	6/	5/	5/	5/	5/	5/	5/	5/	5/
Inner flagellum: segments/ setae	0.5(5), (4)0	0.5(5), (3)0	-	0.6(5), (3)0	0.4(4), (3)0	0.6(6), (4)0	0.6(6), (4)0	0.5(5), (3)0	0.5(5), (3)0	0.5(5), (3)0	0.5(5), (3)0	0.5(5), (3)0	0.5(5), (3)0	0.5(5), (3)0	0.5(5), (3)0
ANTENNA															
Flagellum: segments	10	7-10	7-9	10	11	10-11	10	8	11	11	9	10	13	13	12
MANDIBLE															
MAXILLULE															
Basal endite	18-21	18-20	-	-	18-20	22	-	18	-	-	19	-	-	-	-
Endopod: segments/ setae	1+1	1+1	-	1	1	1	1	1+2	-	1+2-3	1+1-2	-	1	1	-
MAXILLA															
Coxal endite	25-32+7-9	27-29+7-8	-	-	27+6	27-30+6-7	-	19	-	-	-	-	-	-	-
Basal endite	8-10+11-13	9-12+10-13	-	-	8+15	10-12+10-15	-	14	-	-	-	-	-	-	-
Endopod: segments/ setae	0	0	-	0	0	0	0	0	-	0	0	0	0	0	0
Scapognathite	50-58+1	47-52+1	-	49-55	60	52	45-60	45	-	50	-	-	-	-	54-56
FIRST MAXILLIPED															
Basal endite	18-21	19-21	-	-	20	15-16	-	15	-	-	-	-	-	-	-
Endopod: segments/ setae	Unseg./0	Unseg./0	Unseg./0	Unseg./0	Unseg./0	Unseg./0	Unseg./0	Unseg./3+6	Unseg./0	5/-,-,-,-4	Unseg./8-12	Unseg./11	Unseg./-	Unseg./-	Unseg./10
SECOND MAXILLIPED															
Basal endite	3	2-3	-	2	3	0 or 2-3	-	-	-	5(part.7)/-	-	-	-	-	-
Endopod: segments/ setae	4/2,3,7-8	4/2,2,3,7-9, 6-7	-	4/1-2,2,-,-	4/-,-,4,6	4/2,2,3,4,6,7	4/1,3,1,3,1,3,-	5/4,2,3,5,6	-	-	-	-	-	-	-
THIRD MAXILLIPED															
Basal endite	6-7+3-4sub-ac-pr	5-7+3-4sub-ac-pr	-	4+	2-3	4+1-2sub-ac-pr	+2-4sub-ac-pr	2sub-ac-pr	-	-	3+	-	-	-	-
Endopod: segments	5	5	Present	5	5	5	5	5	-	7	5/2+2,2+1,4+1,-,-	-	-	-	-
Endopod: <i>crista dentata</i>	2/1,6-8	2/1,8	-	2/1,8	-	2/-	2/0,6	2/-6	Present	3/-,6	Unseg./6	-	-	-	-
PERIOPODS															
First: chelipeds	Equal	Equal	Equal	Equal	Equal	Equal	Equal	Equal	Equal	Sub-equal	Sub-equal	Sub-equal	Sub-equal	Sub-equal	Sub-equal
Second/ third: dactyl spines	14-16/17-18	10-14/11-15	-	3	-	3-4	3	-	-	3	2-3	4	-	-	-
Fourth/ fifth: propodal pc	Decr. post.	Decr. post.	Decr. post.	Decr. post.	Decr. post.	Decr. post.	Decr. post.	Decr. post.	Decr. post.	Decr. post.	4-6/-	-	-	-	-
UROPODS															
Endopod: setae	10-11+7-8pc	8-9+7-8pc	7-8+6-8pc	11-14+5-7pc	12-20+6-7pc	8-10+5-6pc	9-13+8-10pc	9+	-	-	-	-	-	-	-
Exopod: setae	17-19+10-13pc	16-18+9-11pc	-	19-21+8-12pc	16-19+11-13pc	11-14+5-6pc	16-19+11-13pc	18+	-	-	-	-	-	-	-
TELSON															
Setae: marginal/lateral/distal	10-11/2 pairs/10-12	8-9/2 pairs/10	-	10/1-2 pairs/9	-	-	-	-	-	6/2 pairs/9	6/2 pairs/9	5/-9	-	-	-

Unseg. unsegmented; unir. uniramous; seg. segmented; bir. biramous; part. partially; sub-ac.pr. sub-acute processes; pc. pseudochaetae; decr. post. decreasing in size posteriorly (1) Pike and Williamson (1960); (2) Le Roux (1966); (3) Dechance and Forest (1958); (4) Siddiqui et al. (1991); (5) Lang and Young (1977); (6) Brossi-Garcia (1987); (7) Siddiqui et al. (1993); (8) Tirmizi and Siddiqui (1979); (9) Shenoy and Sankolli (1977); (10) Nayak (1984); (11) Shenoy and Sankolli (1975); (12) Ajmal Khan et al. (1981); (13) Ajmal Khan and Natarajan (1981a); (14) Ajmal Khan and Natarajan (1981b). Numbers in parenthesis: number of aesthetascs. If not otherwise indicated, the given numbers represent the respective setation formula

posterolateral angles rounded; the telson has a rounded posterior margin, with 5–11 setae. Usually, the megalopa has symmetrical chelipeds, and an apically curved and corneous dactylus in the second and third pereopods. Although Shenoy and Sankolli (1977) reported the presence of ocular acicles as a generic character for the megalopa, these structures can be reduced or even absent in some species (see Table 1).

Regardless of the general larval morphology homogeneity in *Clibanarius*, there is some variation among congeneric species. These relate to the telson formula and to the morphology of the telson processes beyond the second larval stage, as well as to the number of zoeal stages.

Shenoy and Sankolli (1977) stated that the telson of the fourth zoeal stage always bears $8 + 1 + 8$ processes, except for *C. erythropus* where it bears $9 + 9$ processes. However, the available data indicate that the latter telson formula can also be displayed by another two species: *C. aequabilis* with $10-9 + 9-10$ processes in zoea III and $9 + 9-10$ processes in zoea IV, and *C. vittatus* with $8 + 1 + 8$ or $9 + 9$ processes in zoea III and $9+9$ processes in zoea IV (Table 1). All these three species are from the North Atlantic Ocean (*C. aequabilis* and *C. erythropus* from the northeastern coast and *C. vittatus* from the northwestern coast). Thus, the telson formula may be related to geographic distribution, since only the above three species acquire an inner pair of plumose setae in the third zoeal stage and not only a single median plumose seta. *Clibanarius vittatus* can present both types of telson formula and that *C. aequabilis* can also present an uneven number of telson processes on the terminal margin of the telson. Therefore, telson development in *Clibanarius* apparently shows some intraspecific plasticity, a feature already highlighted by other authors (e.g. Barria et al. 2006).

Concerning the fourth telson process as a fused spine, beyond the second larval stage, this fused spine can be either well developed (*C. albidigitus*, *C. antillensis*, *C. merguiensis*, *C. virescens* and *C. vittatus*), or reduced (*C. aequabilis*, *C. erythropus*, *C. clibanarius*, *C. infraspinitatus*, *C. longitarsus*, *C. olivaceus*, *C. padavensis*, *C. scolopetarius* and *C. signatus*). Shenoy and Sankolli (1977) considered this reduced fused spine a generic feature of *Clibanarius* larvae. However, Nayak (1984) later showed that in *C. merguiensis* the fourth telson process is a well-developed fused spine. Therefore, we suggest that it is the transformation of the plumose fourth telson process into a fused spine (either well developed or reduced) in the transition from zoea II to zoea III that should be considered a generic character of *Clibanarius* zoeal stages.

Studies on anomuran larvae generally consider telson processes a very important diagnostic character (e.g. McLaughlin et al. 1992, 1993). Based on the different

formation of the fourth telson process beyond the second zoeal stage, four groups of species can be differentiated within the Diogenidae: group 1 (genera *Calcinus*, *Dardanus*, *Petrochirus* and *Trizopagurus*) with the fourth telson process as a well developed fused spine; group 2 (genus *Clibanarius*) with the fourth telson process either as a well develop or a reduced fused spine; group 3 (genus *Diogenes*) with the fourth telson process as a strongly reduced spine which disappears during larval development; and finally group 4 (genus *Paguristes*) where in all larval stages telson processes are represented by setae. These findings do not give any indication of the polarity of the respective evolutionary changes. In pagurids and diogenids early larval stages, the fourth telson process is articulated and later becomes fused, while the opposite sequence has never been recorded so far. McLaughlin et al. (2004) highlighted the fact that telson processes frequently become fused in paguroids, particularly in members of the family Paguridae. The same evolutionary pattern may therefore be suggested for the Diogenidae (with the exception of the genus *Paguristes*), as indicated by our study.

Finally, the occurrence of a fifth zoeal stage as in *C. olivaceus*, *C. scolopetarius* and *C. vittatus*, does not seem to be the rule among *Clibanarius* species. Siddiqui et al. (1991) recorded the occurrence of four or five zoeal stages in *Clibanarius* and the need of 5 zoeal stages to complete the larval sequence in *C. vittatus*. From the larval sequences of the three species with five zoeal stages (Table 1), we can conclude that in *C. olivaceus* and *C. vittatus* a fifth zoea is absolutely necessary to acquire all the features of a final zoeal stage, while a fifth zoea might be unnecessary in *C. scolopetarius*. Lang and Young (1977) also concluded that the most common developmental series in *C. vittatus* involves five zoeal stages, with stage IV being separated from stage V by the lack of mandibular palp. The larval sequence in *C. scolopetarius* commonly includes four zoeal stages, and when a fifth zoeal stage appears, zoea III already exhibits a biramous antennule (Brossi-Garcia 1987). Due to the morphological similarity displayed by the fourth and fifth zoeal stages of *C. scolopetarius*, it seems that the occurrence of a fifth zoeal stage might result from a laboratorial artifact. Gore (1985) reported how unsuitable rearing conditions may favour the appearance of extra and intermediate larval stages. Another explanation for the occurrence of a fifth zoeal stage may be interspecific variation (Ajmal Khan and Natarajan 1981b). Furthermore, since *Clibanarius* larvae can easily delay metamorphosis (Harms 1992; Harvey 1996), the absence of adequate settlement cues might be another factor favouring the occurrence of extra zoeal stages in laboratory cultures.

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